

REVISION OF THE MARINE SPONGE GENUS *AXOS* GRAY (DEMOSPONGIAE: AXINELLIDA) FROM NORTH-WEST AUSTRALIA

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ABSTRACT

The Australian marine sponge genus *Axos* Gray (Hemiasterellidae) is revised. Two species are recognised, *A. cliftoni* Gray and *A. flabelliformis* Carter, and are differentiated on the morphology of euaster microscleres. Reproductive products of *A. cliftoni* are described. *A. spinipoculum* Carter is redescribed from the holotype and transferred to *Latrunculia* Bocage. The holotype of *A. anchorata* Carter, and recent specimens of *A. fibulata* Carter are described, and the species are retained in *Plumocolumella* Burton and *Gelliodes* Ridley, respectively, following Burton (1934). The family Hemiasterellidae is reviewed.

KEYWORDS: taxonomy, Porifera, Axinellida, Hemiasterellidae, *Axos*, north-west Australia.

INTRODUCTION

The genus *Axos* Gray is an aster bearing marine axinellid sponge, which has suspected Hadromerid affinities. The genus was revised in a footnote by Burton (1934: 549) presumably based on original material, but no descriptions or other evidence was presented by that author. Species are prevalent in northwest Australian waters, and indeed they appear to be restricted to this region. This paper revises *Axos* from type specimens and recent material from the Northern Territory and Western Australia, and discusses the family Hemiasterellidae.

Methods of preparation and examination are described elsewhere (Hooper 1984a, 1984b). Scanning electron micrographs of euasters were obtained from sponge sections dissolved directly onto microscope cover glasses, in nitric acid and heat. Cover glasses were mounted on stubs and vacuum plated in gold. Spicules were measured using a camera lucida and calibrated digitizer (computer graphics pad). Analyses of variance (Rx2 ANOV) and Student's t-tests were computed following the methods and models prescribed by Steele and Torrie (1960) and Zar (1974).

Abbreviations used in the text are as follows: AM Australian Museum, Sydney; BMNH British Museum (Natural History), London; LFM Merseyside County Museums (formerly Liverpool Free Museum), Liverpool; NMV Museum of Victoria (formerly

National Museum of Victoria), Melbourne; NTM Northern Territory Museum, Darwin; WAM Western Australian Museum, Perth; ZMA Zoological Museum, Amsterdam.

SYSTEMATICS

Family Hemiasterellidae Lendenfeld

Hemiasterellinae Lendenfeld, 1889: 903.
Hemiasterellidae — Lévi 1973: 606; Bergquist 1978: 67; Wiedenmayer 1977a: 152; Hartman 1982: 647.
Astraxinellidae Dendy, 1905: 107; Stephens 1912: 59, 1915: 28; Topsent 1919: 6, 1928: 38; Wilson 1925: 354; Lévi 1955: 79.

Diagnosis. Sponges incrusting, digitate, arborescent, flabelliform, cup-shaped or vaseiform. Monactinal, occasionally quasi-diactinal or diactinal megascleres enclosed in spongin fibres or spicule tracts, with or without ectosomal specialization. Choanosomal fibres and tracts form a condensed or plumoreticulate extra-axial skeleton. Microscleres smooth or microspined euasters (Lendenfeld 1889; Lévi 1955; Hartman 1982).

Remarks on genera included in the family. Hemiasterellidae was established for *Hemiasterella* Carter and *Epallax* Sollas (not Gray; cf. de Laubenfels 1936; Wiedenmayer 1977a), with brief diagnosis "Axinellidae with stellate microsclera" (Lendenfeld 1889: 903). The possession of euaster microscleres is the principal feature differentiating Hemiasterellidae from other Axinellida. The presence of euasters in other tetrac-

tinomorph groups (orders Astrophorida (Choristida) and Hadromerida), probably represents the retention of an ancestral character, and all three groups may have arisen from a common ancestor (c.g. Astrotetragonid stock (Reid 1970: 79)). Consequently, those taxa cannot be discriminated on that basis. Similarly, there is a paucity of other morphological (skeletal) characters, of known stability, available for classification of those taxa. It remains to be investigated whether shared morphological features (megasclere and microsclere spiculation, growth form, and skeletal architecture) are indicative of true affinities between groups (in preparation).

The present definition of Hemiasterellidae is unsatisfactory, as it relies upon the possession of an ancestral character to differentiate it from other Axinellida. No solution is presently available without a re-evaluation of all tetractinomorph orders. Hemiasterellidae presently comprises the following genera.

1. *Hemiasterella* (type species *H. typus* Carter, 1879: 146) contains a diverse group of taxa in which megascleres are monactinal, diactinal, or a combination of both; the architecture is more-or-less plumo-reticulate, and growth form is exclusively vasiform or cup-shaped (Topsent 1919: 6; Dendy 1922: 144). *Hemiasterella s.s.* has monactinal megascleres, and as such shows affinities with *Axos* and *Timea*. *Hemiasterella s.l.* includes taxa bearing oxeas only (e.g. *H. affinis* Carter, 1879: 147), or both oxeas and styles (e.g. *H. complicata* Topsent, 1919: 7). In that respect, the taxon is diverse as *Raspailia* Nardo *s.l.*, and some species are morphologically very close to *Jaspis* Gray (type species *Vioa jolmstoni* Schmidt, 1862: 78) of the Coppatiidae Topsent (syn. Jaspidae de Laubenfels) (e.g. Bergquist 1968: 33; Wiedenmayer 1977a: 173).

Indeed, de Laubenfels (1936) placed several Hemiasterellids with the Coppatiidae but Wiedenmayer (1977a: 152) suggests that despite apparent morphological congruence, such a system totally disregards characters such as architecture and growth form, and that affinities of those taxa are with the Axinellida. Although it remains to be demonstrated that those attributes are of primary importance at the ordinal level of classification, de Laubenfels system cannot be upheld. It is probable however, that sev-

eral *Jaspis* (syn. *Coppatias* Sollas, type species *C. coriaceus* (Carter, 1886: 126)) will be transferred to hemiasterellid genera, particularly those species without obvious radial architecture, and modified oxeote megascleres (strongyles, stonyloxeas and quasi-monacts) (e.g. *Coppatias carteri* (Ridley, 1884).

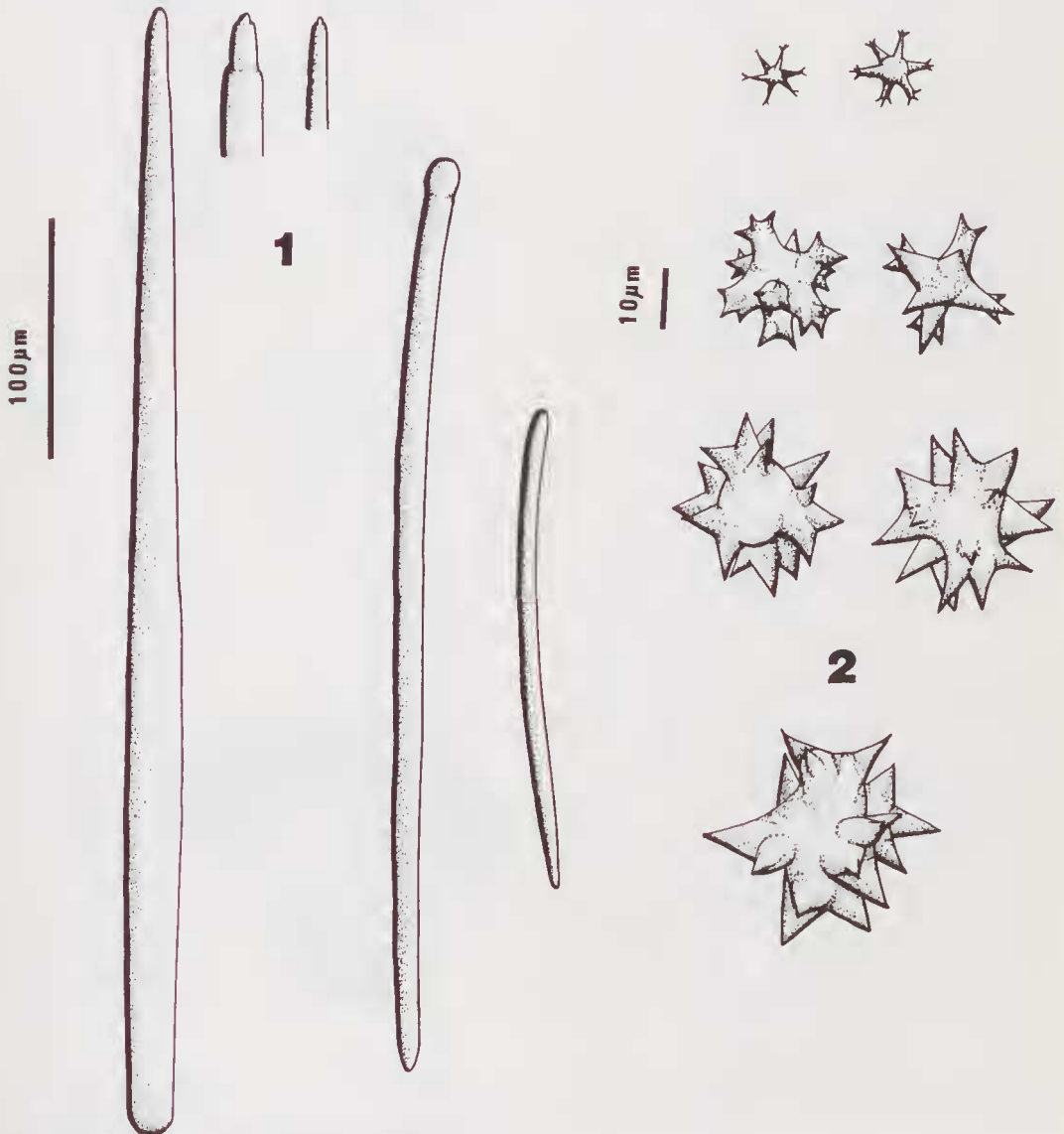
2. *Epallax* Sollas (type species *E. callocyathus* Sollas, 1888: 423) is vasiform also, has diactinal megascleres, which are occasionally modified to quasi-monactinal styles or tylostyles, and an architecture consisting of longitudinal bundles of megascleres in a more-or-less radial arrangement. By those characters, *Epallax* is virtually identical to *Hemiasterella s.l.*, and as such Topsent (1919) and Dendy (1922) include the type and only species with *Hemiasterella*. *E. callocyathus* has, in addition to simple oxyasters common to other Hemiasterellids, calthrops-like asters, for which Sollas (1888) inferred parallels with the genus *Thenea* Gray (Order Astrophorida). Similarly, *Epallax* should be compared to *Timea*, in which several species have been erected on the sole basis of possessing calthrops-like asters (e.g. Pulitzer-Finali 1977, 1983), and *Jaspis* in having a tendency to modify oxcas to quasi-monactinal forms. *Jaspis s.s.* usually has oxyasters as microscleres only (de Laubenfels 1936; Wiedenmayer 1977a), and maintains a radial architecture.

3. Dendy (1905: 107) added *Vibulinus* Gray (type species *V. stuposus* (Montagu)) to his Astraxinellidae (=Hemiasterellidae; Astraxinellidae is *nomen nudum*; there is no genus "*Astraxinella*" (Wiedenmayer 1977a)). The growth form of *V. stuposus* is reminiscent of *Axos cliftoni* Gray (see below), *Raspailia* species, and many other Axinellids (Montagu 1814: 79; Stephens 1914; Pl. 3). *Vibulinus*, *sensu* Bowerbank, has monactinal to quasi-diactinal megascleres (cf. Gray 1867: 545), with a condensed axial skeleton and radial extra-axial skeleton (Bowerbank 1866; Gray 1867). The spiculation of Montagu's (1814) type specimen has not been described, and therefore it is only surmised that Bowerbank's (1866) specimen of *Dictyocylindrus stuposus* is conspecific with Montagu's species. That specimen must be re-examined to corroborate Gray's *Vibulinus s.s.* *Vibulinus s.l.* (e.g. *V. stuposus*, *sensu* Bowerbank 1866 and *V. mutilus* Topsent,

1928: 188) has both monactinal and diactinal megascleres; the former coring the axial skeleton, at right angles to it, and protruding beyond the ectosome, the latter occurring in the extra-axial, peripheral skeleton. In the disposition of its megascleres, *Vibulinus* shows close affinities with Raspailiidae (Axinellida), whereas the presence of oxyasters would suggest affinities with the Hadromerida. *Stelligera* Gray (type species *Raspailia stelligera* Schmidt, 1862: 60) is arborescent to lobodigitate, occasionally flabelliform, and has both oxeas and styles (or tylostyles) as megascleres and euasters as microscleres. It is probable that *Stelligera* is

synonymous with *Vibulinus* (e.g. Topsent 1900: 112; Van Soest pers. comm.), in which case the former name has priority.

4. Topsent (1904: 137, 1919: 7) included *Adreus* Gray (type and only species *Adreus fascicularis* (Bowerbank, 1866: 110)) with the aster-bearing Axinellids. *Adreus* is arborescent, with monactinal megascleres occurring in bundles, ascending towards the periphery, and with apparent size differences between choanosomal and subectosomal megascleres (Bowerbank 1866: 110; Gray 1867: 545; Topsent 1928: 38). Euasters are not abundant, and occur mainly in the

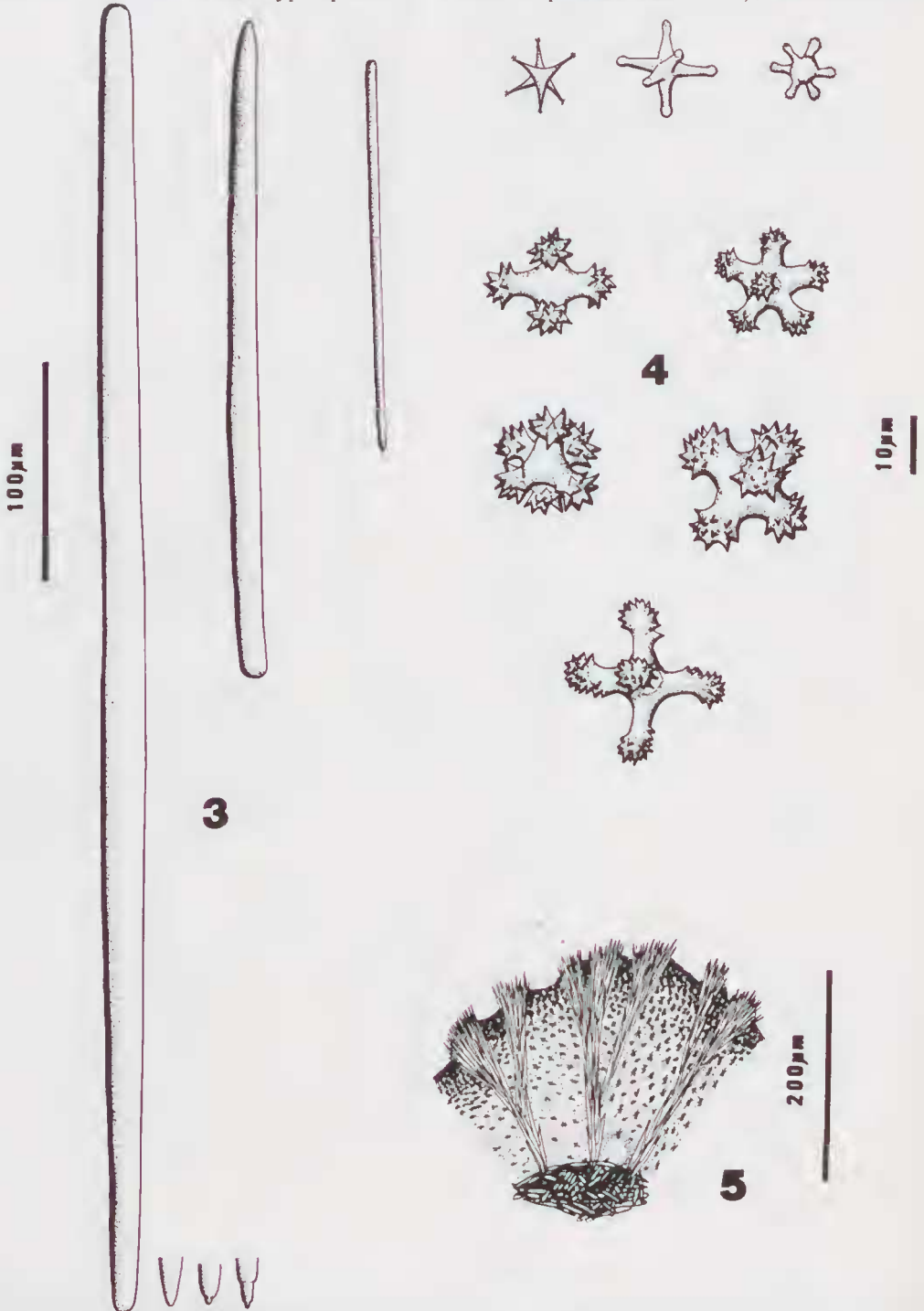


Figs 1-2. *Axos cliftoni* holotype: 1, styles; 2, euasters.

ectosomal region. Sexual reproduction has been reported, and larvae are oviparous (Brien 1973: 303). *Adreus* is closely related to *Axos* and *Stelligera* and possibly synonymous with *Axos*, but Bowerbank's type specimen

must be re-examined to confirm such a combination.

5. Kirkpatrick (1903) proposed the genus *Kalastrella* (type and only species *K. vasiformis* Kirkpatrick, 1903: 238), which is vase-



Figs 3-5. *Axos flabelliformis*: 3, styles, holotype; 4, euasters, holotype; 5, section of peripheral skeleton, NTM Z1031.

shaped, has both monactinal and diactinal/quasi-diactinal megascleres, and microspined rays on euasters (similar to many *Timea* species, order Hadromerida). Skeletal architecture is more-or-less condensed, with interconnected lacunae, which bear extra-axial small bundles of oxeas and styles projecting at right angles to the ectosome (Kirkpatrick 1903). Topsent (1919: 6) and Dendy (1922: 144) consider that *Kalastrella* is a junior synonym of *Hemiassterella*, and is closely related to *H. complicata* Topsent.

6. Hallmann (1916: 673) combined the Desmoxyidae Hallmann (with acanthose or smooth microxeas) and the aster-bearing Axinellids; *Halicnemias* Bowerbank (type species *H. patera* Bowerbank, 1864: 184), *Laonoenia* Hallmann (for *Laothoe* Gray and *Noenia* Gray, both preoccupied; type species *Hymeraphia verticillata* Bowerbank, 1864: 268), and *Paratimea* Hallmann (type species *Bubaris constellata* Topsent, 1893: 33), all of which possess choanosomal tylostyles and ectosomal centrotylote oxeas. Topsent (1928: 38) rejects Hallmann's system and new genera, and retains *Halicnemias*, *sensu* Topsent, in a broad sense (= *Halicnemias* Bowerbank, + *Paratimea* Hallmann + *Laonoenia* Hallmann). *Halicnemias s.s.* (viz. *H. patera*, and including *H. gallica* (Topsent) and *H. geniculata* Sarà) has tylostyles, ectosomal oxeas, often polytylote, and acanthose microxeas (Bowerbank 1864: 363, 1866: 96; Topsent 1897: 235, Descatoire 1966: 238). By comparison, *Halicnemias s.l.* (*H. arbuscula* Topsent, 1928: 185; *H. duplex* Topsent, 1928: 182; *H. azorica* Topsent, 1904: 149; 1928: 181; *H. constellata* (Topsent, 1893: 33; 1897: 245); *H. verticillata* (Bowerbank); and *Paratimea galaxea* de Laubenfels, 1936: 146) has euasters, ectosomal centrotylote oxeas, and choanosomal tylostyles. *Halicnemias s.s.* is correctly assigned to the Desmoxyidae (Lévi 1973), and is close to the genus *Higginsia* Higgin, whereas other nominal species containing asters are better placed in *Stelligera s.l.*, which must be expanded to include incrusting forms.

7. By its skeletal architecture, *Axos* Gray is the most closely related of all the Hemiassterellidae to the Axinellida, and its spiculation is typical of the family (see below).

Of the recognizable Axinellid genera which bear asters, only four can be differentiated on the basis of morphological characters. Genera can be diagnosed as follows. (1) *Hemiassterella* (species examined — none) has a distinctive vasiform habit, without regional differentiation of monactinal and/or diactinal megascleres, and with only slightly condensed plumo-reticulate architecture. (2) *Stelligera* (species examined — *S. stuposa* (Montagu), ZMA POR 5945) has distinctive axial and extra-axial differentiation of megasclere type. The axis is condensed and cored by monactinal megascleres, whereas there are extra-axial plumose to plumo-reticulate columns of monactinal and/or diactinal megascleres. (3) *Adreus* (species examined — none) has monactinal megascleres only, a plumose to plumo-reticulate architecture, and distinctive differentiation in megasclere size between axial and extra-axial regions. Euasters are predominantly peripheral. (4) *Axos* (species examined — *A. cliftoni* Gray, holotype BMNH, *A. flabelliformis* Carter, holotype BMNH) is distinctively digitate, less commonly flabelliform, with prominent surface ornamentation. The skeleton is axially condensed and extra-axially plumo-reticulate, and there is no pronounced regional differentiation of monactinal megascleres.

Genus *Axos* Gray

Axos Gray, 1867: 546 (type species *A. cliftoni* Gray, by monotypy).

Echinospingia Gray, 1870: 272 (type species *E. australis* Gray, 1870, by monotypy). Syn. by de Laubenfels 1936: 161.

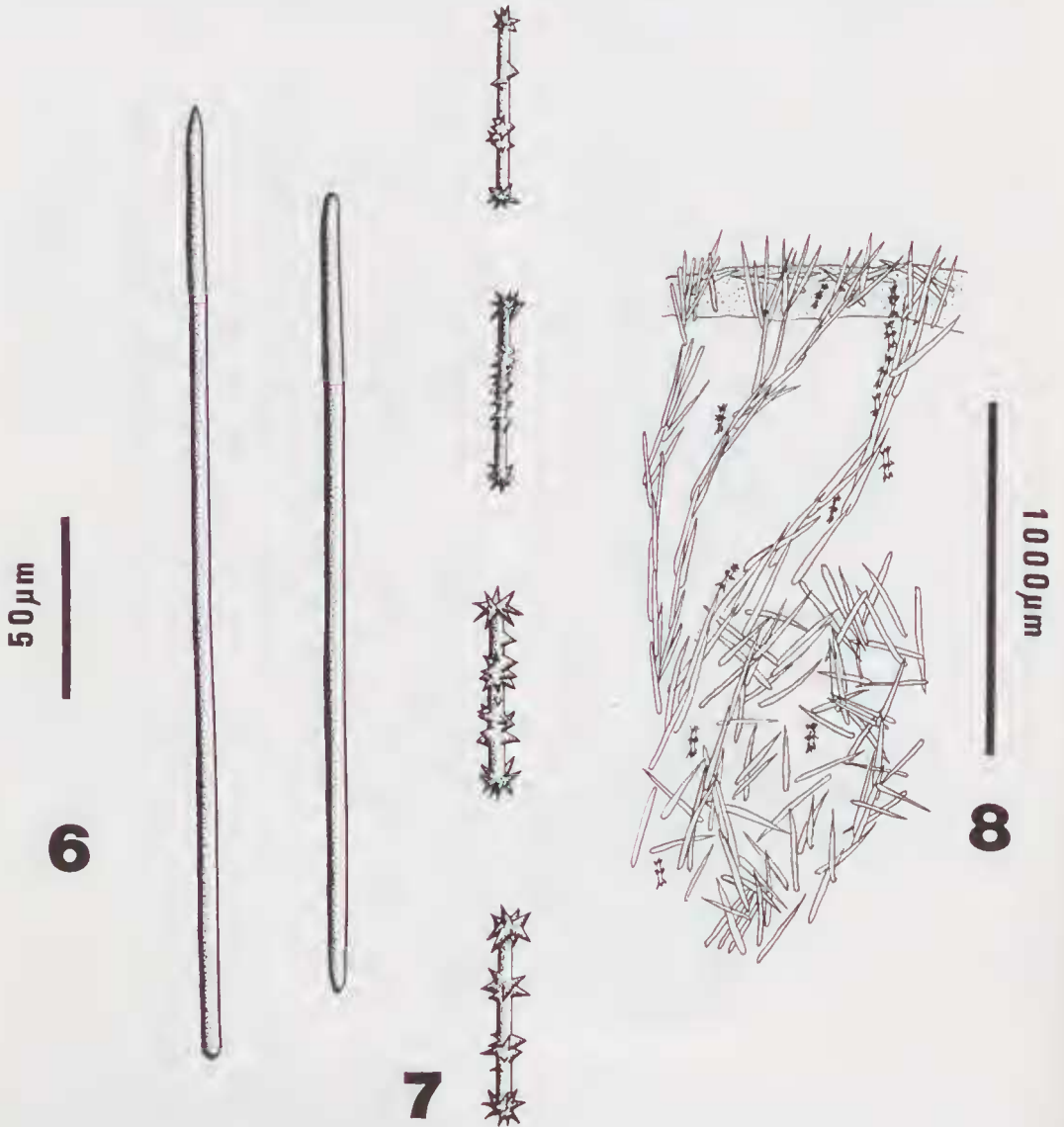
Diagnosis. Digitate, anastomosing or dichotomously branched, to thinly flabelliform growth form. Surface raised into specialized conulose or micropapillose structures, formed by protruding extra-axial components of peripheral skeleton. Choanosomal skeletal architecture condensed, rarely plumo-reticulate. Extra-axial (subectosomal) architecture plumose to plumo-reticulate. Ectosome microscopically hispid, containing dense layers of euaster microscleres. Megascleres styles to subtylostyles. Reproductive pattern oviparous.

Remarks. *Axos* was established for *A. cliftoni* Gray, named for a single spicule depicted by Bowerbank (1864). From its description, *Echinospingia australis* is iden-

tical to *A. cliftoni*, and subject to confirmation from re-examination of the type specimen, *Echinosporgia* becomes a junior synonym of *Axos* (de Laubenfels 1936).

De Laubenfels (1936: 161) suggests further that *Axos* and *Adreus* are closely related, with similar growth form and spiculation. He suggests that the genera are differentiated in having branched rays on the euasters, and a greater proportion of oxeas than styles (*Axos*). That observation is erroneous. *Axos cliftoni* (see below) has monactinal megascleres only, and furthermore in the description of *Dictyocylindrus fascicularis*

(Bowerbank, 1866) it is reported that "acuates" (styles) are present only. The contention that *Adreus* and *Axos* can be differentiated by the presence or absence of a regional size differentiation of choanosomal megascleres between axial and extra-axial regions, respectively, is debatable. That character is also present in *A. cliftoni* and *A. flabelliformis*, although it is not pronounced or obvious. Similarly, the morphology of euasters in the two *Axos* species recognized here, is certainly unusual to either Hemiassterellidae or Timeidae species, but the uniqueness of that character is solely due to



Figs 6-8. *Latrunculia spinipoculum* holotype: 6, styles; 7, verticillate sanidasters; 8, section of peripheral skeleton.

an emphasised microspination, rather than branching of aster rays as suggested by de Laubenfels (1936). Bowerbank's type species of *Adreus* requires redescription prior to a decision on the possible synonymy of *Axos* and *Adreus*; the latter genus has line/page priority over *Axos*. Notwithstanding the possible synonymy (*D. fascicularis* is from the English coast), *Axos* is indigenous to the northwest coast of Australia.

***Axos cliftoni* Gray**

(Figs 1, 2, 13, 18-21, 25, Pl. 1A)

Unidentified sponge — Bowerbank 1864: 260, Pl. 10, Fig. 197.

Axos cliftoni Gray, 1867: 546-7; Ridley 1884: 454; Dendy 1921: 95, Burton 1934: 549.

Non *Axos cliftoni* — Carter 1879: 284, Pl. 26, Figs 5-7.

Dictyocylindrus dentatus Bowerbank, 1873: 321, Pl. 29.

Echinospingia australis Gray, 1870: 272.

Type material. HOLOTYPE - BMNH 1870.8.26.31 (dry: label "523. G. Clifton esq. E.h.21"); 1870.8.26.11 (spicule preparation; "No. 8A").

Additional material. BMNH 1930.12.1.10a (spicule preparation; label "Pres. Mrs B. Gray, Cape Boileau, NW Australia"); BMNH unreg (holotype of *Dictyocylindrus dentatus* Bow.; photograph NMV 41/8-10 sponge archives — F. Wiedenmayer); NTM Z1274, North of Bedout Island, NW Shelf, Western Australia, 19°33.1'S 118°43.8'E, 26 April 1983, 35 m depth, coll. J.N.A. Hooper, RV "Soela" SO2/83, trawl; NTM Z1424, Northeast of Port Hedland, NW Shelf, WA, 19°01'S 119°25'E, 19 April 1983, 80 m depth, coll. R.S. Williams, FV "Tung Mao I", trawl; NTM Z1821, West of Port Hedland, NW Shelf, WA, 19°26.9'S 118°54.2'E, 30 August 1983, 50 m depth, coll. T. Ward, RV "Soela" SO4/83, stn.126, trawl.

Distribution. Type locality: Nickol Bay, Dampier Archipelago, NW Shelf, WA (20°30'S 117°00'E) (Bowerbank 1864; Gray 1867, 1870). In the present study the species was recorded only in the Port Hedland region, approximately 200 km from the type locality. The species appears to be extremely restricted in its distribution.

Ecology. Attached to dead coral, rock or shell grit conglomerate; basal portion par-

tially burrowed into substrate. Bathymetric distribution 35-80 m depth.

Description of holotype. Fragment of branch, thickly cylindrical, with large surface conules. Original specimen probably digitate, anastomosing or dichotomously branched growth form. Texture firm, incompressible in dry state. Colour white-beige. Surface smooth between conules. Pores and oscula minute, inconspicuous.

Ectosome: contains dense deposits of euasters, with ascending plumose columns of choanosomal/subectosomal styles poking through surface at tips of conules. Ectosome dense, not opaque, and paper-like in dry state. Subectosomal region contains occasional plumose tracts of styles arising from choanosomal skeleton, associated with surface conules, and scattered euasters between tracts. Collagenous non-fibre spongin abundant, moderately heavy. Subdermal cavities and choanocyte chambers obscured by mega- and microscleres.

Choanosome: skeleton has a dense axial core of reticulated megascleres, mostly running longitudinally through branches, less often giving rise to extra-axial (subectosomal) plumose tracts of megascleres. Fibre component of axial skeleton not observed; if present, it is completely cored by styles.

Megascleres: Smooth, fusiform, rounded or stepped styles, mostly straight, occasionally slightly curved near basal end. (N=25) Length 517.68 μm (mean) (range 217-851 μm), width 9.04 μm (2-15 μm).

Microscleres: Euasters, variable in morphology, relatively large, hexaradiate to cruceiform, often with asymmetrical spination. No or little tylote swelling on apices of rays. Spines large and distributed over tips of rays. (N=25) Maximum mean diameter 23.36 μm (12-29 μm).

Description of other specimens. BMNH 1930.12.1.10a.

Megascleres: identical to holotype. (N=25) Length 428 μm (mean) (range 208-670 μm), width 7.32 μm (2-12 μm).

Microscleres: identical to holotype. (N=25) Maximum mean diameter 17.16 μm (8-26 μm).

NTM specimens (N=3).

Colour. orange-red to red-brown alive (Munsell 2.5R 4-5/4-8-5R 6/12) (Pl. 1A). Pigment alcohol soluble, and preserved specimens grey to being in colour.

Shape: Dichotomously branched, occasionally digitate anastomosing, with basal stalk and holdfast attachment. Attachment rhizomous, adhering to shell and gravel particles. Branches thickly cylindrical, rubbery in appearance, with large, rounded surface conules; average diameter of branches 7-22 mm (mean 13.6 mm) excluding conules, 15-35 (mean 23.3 mm) including conules. Basal stalk hard, woody in texture, 14-26 mm (mean 18.3 mm) in diameter. Branching pattern multiplanar. Specimens range in size from 60-65 cm (mean 63 cm) total length, from basal attachment to apex of branches.

Texture: rubbery, tough, difficult to cut; stalk rigid, branches compressible.

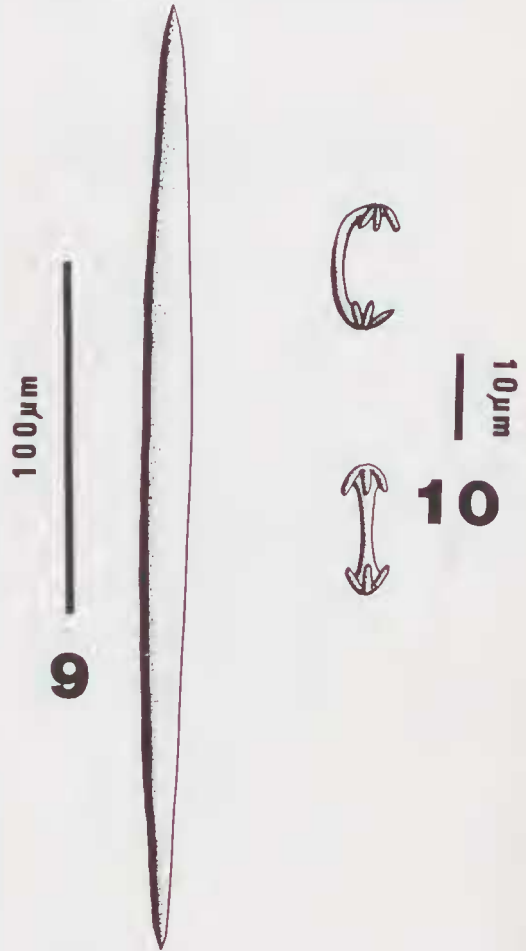
Surface characteristics: optically smooth between conules, with evenly distributed, tapering conules with rounded apices. Conules range from 4-12 mm (mean 8.6 mm) in length, 3-8 mm (mean 6.4 mm) basal diameter. Oscula minute (0.2-0.8 mm diameter in preserved specimens), and distributed evenly over surface. Surface between conules microscopically hispid and rugose, composed of interconnected ridges.

Ectosome: dense, relatively easily detached, containing heavy concentrations of euasters. Ectosome pierced at regular intervals (0.5-1.0 mm apart) by ascending tracts of choanosomal/subectosomal (extra-axial) styles. These hispidating megascleres form a more-or-less continuous but light dermal palisade. Ectosomal spongin heavily pigmented.

Choanosome: peripheral (subectosomal) skeleton is moderately dense, containing plumose, non-anastomosing extra-axial tracts of styles, which radiate from the axial core, between which are scattered euasters. Collagenous spongin abundant and heavily pigmented, but mostly obscured by euasters. Subdermal cavities not observed (except in 1 specimen — NTM Z1424; see below). Extra-axial spicule tracts between 60-110 μm in diameter, cored with up to 8 rows of spicules. No fibre-spongin visible surrounding spicules. Choanocyte chambers oval, 12-42 μm in diameter, and mostly obscured by euasters. The peripheral skeleton occupies up to 66% of branch diameter, decreasing towards the stalk and branch tips. Central axis is massive, irregular in cross-section, and irregularities correspond to the distribution

of surface conules. Axis consists entirely of styles, tightly packed together, and mostly running longitudinally along branches. Occasional extra-axial tracts diverge from the axial core, usually at right angles to it, and ascend towards the periphery. No choanosomal fibres observed, and if present, they are hidden totally by dense aggregation of styles at the core. There is a suggestion of regional (axial versus extra-axial) differentiation of megascleres, whereby the peripheral skeleton has larger, thicker megascleres, but this is not distinctive, or easily discerned.

Megascleres: fusiform styles, straight or slightly curved near base, with sharply pointed or rounded apices, occasionally stepped. Bases smooth, rounded and non-tylote. (N=75) Length 474.59 μm (mean) (range 178-912 μm), width 11.07 μm (1.5-22 μm).



Figs 9-10. *Plumocolumella anchorata* holotype: 9, oxea; 10, unguiferous anchorate isochelae.

Microscleres: euasters of very variable morphology, and relatively large diameter. Shape ranges from hexaradiate to true stellate, less commonly cruciform. Rays non-tylote and bear large spines at tips. Distribution of rays often asymmetrical. (N=75) Maximum mean diameter 24.27 μm (8-37 μm).

Reproduction. Sexual reproductive products were recorded for one specimen of *A. cliftoni*. The species appears to be oviparous, and parenchymella larvae were recorded in April 1983 (NTM Z1424). Larvae are solid, oval, white to pale yellow (preserved) parenchymella, 0.5-0.8 mm in diameter (Fig. 25). Cilia were not observed (preserved material), but juvenile megascleres and microscleres are abundant at the posterior pole. A peculiar behaviour is indicated, whereby a large population of larvae occur on the external surface of the sponge, predominantly on the lower part of branches and basal stalk. No embryos were found below the ectosome, nor where they observed in the deeper choanosomal regions, but subdermal cavities were relatively numerous (up to 1 mm in diameter). Larvae appear to be in contact with the adult, but not attached to it. It is speculated that attachment to the parent may involve a mucous envelope (oocyte strands) surrounding the parenchymella, released by the adult along with the larvae, as described by Reiswig (1976) for *Agelas* and *Hemectyon* (Axinellida).

These observations can be interpreted in several ways. It is possible that larvae resident on the external surface of the adult are foreign to the sponge, using it merely as a substrate for settlement. Larval spicules present (thin wispy styles and small euasters) are clearly of *Axos* origin, and that hypothesis is unlikely. Alternatively, it seems plausible that eggs have been extruded by the adult, together with gelatinous oocyte strands (e.g. Reiswig 1976), and the subsequent larval development is external to the sponge. The abundance of larvae resident on the external surface poses questions as to the duration of their association with the "parent", and the age of those larvae, all of which appear to be of similar developmental morphology.

Comparable reproductive strategies for the Hadromerida and Axinellida have been reported by Lévi (1956), Reiswig (1976) and Bergquist (1978).

The specimen of *A. cliftoni* recorded here with reproductive products was obtained from a relatively deep, isolated locality. No other reproductive activity has been recorded for this species, nor for the closely related, and more abundant *A. flabelliformis* (see below), despite a relatively widespread local distribution for both species, and repeated observations and collections over several seasons by the author.

Remarks. *A. cliftoni* s.l. has two distinct euaster morphologies (Figs 18-24). The first morph (Figs 18-21) is identical to the holotype, and to Bowerbank's (1864) figure. Figures of *Dictyocylindrus dentatus* and *Echinosporgia australis* (Bowerbank 1873; Gray 1870) depict the same form of euaster as *A. cliftoni* s.s., viz. asymmetrical, large spines on aster rays, and a statistically larger size than the other morph (Table 1). For this reason, and other morphological attributes (growth form, megasclere size), those species are considered as junior synonyms of *A. cliftoni* s.s.

The second euaster morph (Figs 22-24) is much more symmetrical, mostly hexaradiate, with minutely spined euaster rays, and microscleres are significantly smaller ($F=95.81$, $P < 0.0005$) than those of *A. cliftoni* s.s. That morph is identical with *A. flabelliformis* s.s. (Carter 1879; holotype BMNH 1883.1.25.8; see below). *A. cliftoni*, sensu Carter (1879: 284) and Barnard's (1879) figures depicting the Northern Territory specimen (labelled *A. elegans* by Lendenfeld (BMNH 1886.8.25.557)) have identical euasters to *A. flabelliformis* s.s. Despite differences in growth forms (the holotype of *A. flabelliformis* is thin, flabelliform; other specimens listed above are digitate, dichotomously branched, cylindrical sponges), those specimens are considered here to be synonymous. Thus, *A. cliftoni* is restricted to specimens with euasters bearing large-spined rays, whereas *A. flabelliformis* has minutely spined, more-or-less hexaradiate and symmetrical asters. Morphometric differences between these closely allied species are summarized in Table 1.

Euasters of *A. cliftoni* superficially resemble chiasters of *Timea* (*Hymedesmia*) *trigonostellata* (Carter, 1880: 52) and *T. granulata* Bergquist, 1965: 186, whereas those of *A. flabelliformis* resemble *Tethya* sp. (Bergquist 1978: Pl. 6A). Consequently,

there are few grounds to accept de Laubenfels (1936) arguments on the uniqueness of *Axos euasters*.

***Axos flabelliformis* Carter**

(Figs 3-5, 14, 16, 17, 22-24, Pl. 1B-D)

Axos flabelliformis Carter, 1879:285-286, Pl.26, Figs 1-4; Carter 1882:362; Burton, 1934:549. Unidentified sponge — Barnard 1879:14-15, Pl.1, Figs 5-7.

Axos cliftoni (part) — Carter 1879:284, Pl.26, Figs 5-7.

"*Axos elegans*"; label name, in Lendenfeld's hand, of specimen (BMNH 1886.8.25.557) from the Northern Territory, presumably the one figured by Barnard (1879).

Type material. HOLOTYPE - BMNH 1883.1.25.8 (dry; label "E.h. 20e"; photograph NMV 41/11 sponge archives — F. Wiedenmayer).

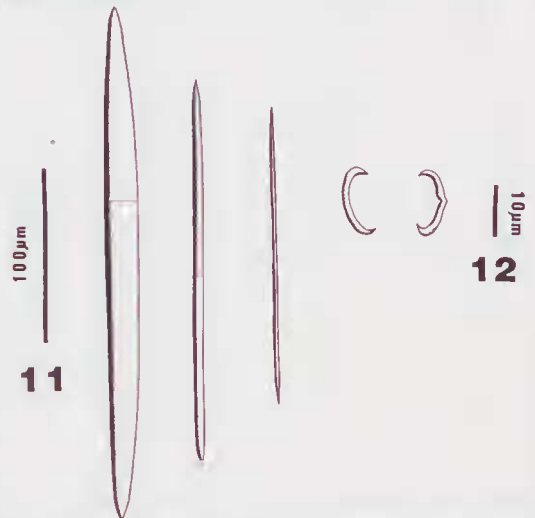
Additional material. BMNH 1886.8.25.557, "*Axos elegans*"; (photograph NMV 40/25 sponge archives — F. Wiedenmayer); NTM Z149, Sandy Island No.2, Cobourg Peninsula Marine Park (CPMP), Northern Territory (NT), 11°05.5'S 132°17'E, 21 October 1981, 10 m depth, coll. J.N.A. Hooper, SCUBA; NTM Z2499, Coral Bay, Port Essington, CPMP, NT, 11°09.4'S 132°04'E, 13 September 1985, 7 m depth, coll. A. Hoggett, SCUBA; NTM Z2505 (3 specimens), NW of Table Head, Port Essington, CPMP, NT, 11°13.5'S 132°10.5'E, 14 September 1985, 3 m depth, coll. J.N.A. Hooper, SCUBA; NTM Z2055, East Point Fish Reserve, Darwin, NT, 12°25.0'S 130°48.4'E, 10 May 1984, 6 m depth, coll. J.N.A. Hooper, SCUBA; NTM Z2084, 20 July 1984, 7 m depth; NTM Z2699, Z2690, 2 April 1986, 9-12 m depth; WAM 143-82, 15 nautical miles NW of Port Hedland, NW Shelf, Western Australia (WA), 20°12'S 118°25'E, 3 August 1982, 14 m depth, coll. J. Fromont, RV "Soela" S04/82, stn 09, trawl (fragment NTM Z1705); NTM Z1031, NW of Dampier Archipelago, NW Shelf, WA, 20°20'S 117°28'E, 22 October 1982, 26 m depth, coll. J. Blake, RV "Soela", shot 64, trawl; NTM Z1168, North of Bedout I., NW Shelf, WA, 19°29.6'S 118°52.2'E, 26 April 1983, 38 m depth, coll. J.N.A. Hooper, RV "Soela" S02/83, stn B8, epibenthic sled; NTM Z1216, 1261, 19°28.5'S 118°55.3'E, 26 April 1983, 40 m depth, stn B9, beam trawl; NTM Z1270, 1271, 1273,

19°33.1'S, 118°43.8'E, 26 April 1983, 35 m depth, Frank and Bryce trawl; NTM Z1756, West of Port Hedland, NW Shelf, WA, 19°03.3'S 118°49.9'E, 29 August 1983, 82 m depth, coll. T. Ward, RV "Soela" S04/83, stn 121, trawl; NTM Z1792, 19°04.1'S 118°57.9'E, 29 August 1983, 84 m depth, stn 124; NTM Z1822, 19°26.9'S, 118°54.2'E, 30 August 1984, 50 m depth, stn 126; NTM Z1871, 19°05.7'S 118°57.4'E, 1 September 1983, 83 m depth, stn 133; NTM Z1886, 19°02.2'S 118°04.1'E, 1 September 1983, 84 m depth, stn 136; NTM Z2299, NW of Lacepede Is., NW Shelf, WA, 16°29-33'S 121°27-29'E, 17 April 1985, 38-40 m depth, coll. B.C. Russell, BYLA "Pao Yuan No.1", pair trawl.

Distribution. Type Locality: unknown, suspected to be "Australia" (Carter 1879). Other: Northern Territory, coll. Dr C. Sturt (Barnard 1879). In the present study the species is recorded throughout Northwest Australia.

Ecology. Attached to dead coral, rock or shell grit conglomerates; basal portion rhizomous in soft substrate, or encrusting on hard substrates. Bathymetric range is intertidal (3 m) to deeper offshore waters (84 m).

Description of holotype. Flabelliform, paper-thin, with aculeated surface formed by minute papilliform projections and longitudinal ridges. Sponge 12 cm high, 11.5 cm long, 3 cm thick, with basal attachment and small basal stalk. Texture cork-like in dry state, and colour white to brownish. Pores not observed.



Figs 11-12. *Gelliodes fibulatus*, NTM Z1050: 11, oxeas; 12, centrangulate sigmas.

Ectosome: packed with euasters, without projecting subectosomal megascleres, although some choanosomal spicules pierce the surface. Ectosome opaque and very thin in the dry state.

Subectosome: region has few plumose (extra-axial) traets of megascleres.

Choanosome: axial condensation of anastomosing spongin fibres, lightly invested with spongin, cored by uni- or paucispicular tracts of styles. Fibres are probably not composed of type A spongin but merely type B (interfibril) spongin, which has contracted in the dry state around megascleres. Fibre diameter ranges from 6-12 μm (mean 8.8 μm). Few loose megascleres were observed between fibres, or in the subectosomal region. Choanocyte chambers not conspicuous, but subdermal cavities scattered throughout the subectosomal region, ranging from 25-110 μm (mean 56.8 μm) in diameter.

Megascleres: smooth, straight or slightly curved styles, with varying apices, from rounded (styloid) to stepped tips, occasionally hastate. (N=25) Length 385.12 μm (mean) (range 193-691 μm), width 7.12 μm (2-12 μm).

Microscleres: euasters, variable in morphology, relatively small, usually hexaradiate or cruciform, in 2 planes, with slightly tylote endings of rays, and mostly profusely microspined. (N=25) Maximum mean diameter 14.08 μm (range 9-21 μm).

Description of other specimens. NTM specimens (N=21).

Colour: most commonly orange to orange-red alive (Munsell 10R 5-6/10-12). Ectosome silt-covered in subtidal specimens *in situ*, with a fine trace or lace-like pattern radiating from minute oscula, clear of silt. Pigmentation mostly even, except in some deeper water specimens, which have more darkly pigmented conules than remainder of ectosome. Colouration variable, unstable, ranging from bright red (5R 5/10) (Pl. 1B), orange (10R 5/10) (Pl. 1C), dark brown (5YR 4/4), grey-yellow (2.5Y 7/4), to beige (2.5Y 8/2) (Pl. 1D) alive. Colour variability may be related to bathymetric distribution, but not definitely so: subtidal specimens invariably have orange to orange-red pigmentation; deeper-water specimens more variable. Pigments are alcohol soluble, and preserved specimens are grey to beige in colour. Caro-

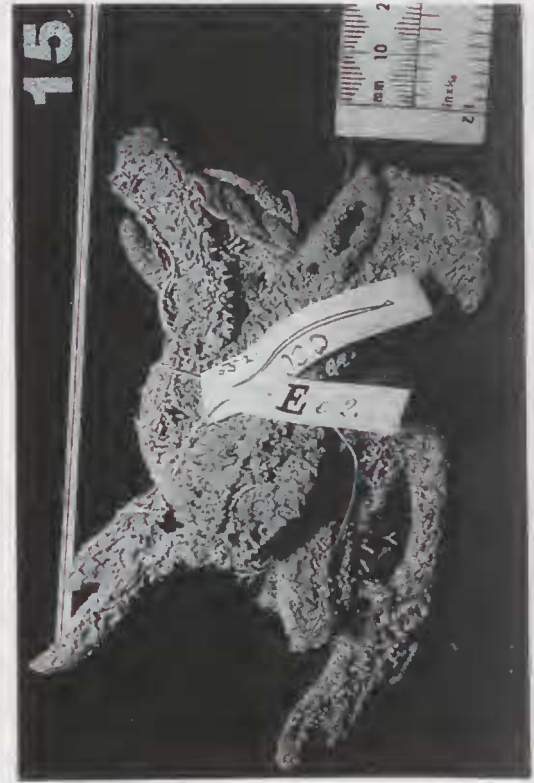
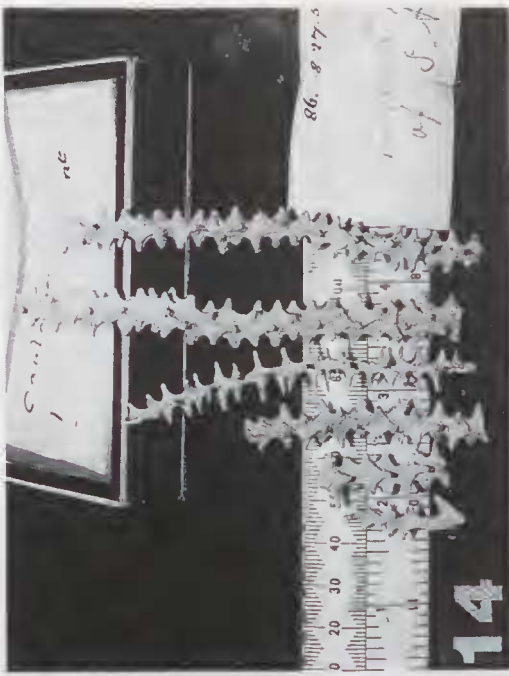
tenoid pigment characteristics of the typical colour form are shown in Fig. 17.

Shape: characteristically arborescent, stipitate, with thick basal stalk and holdfast attachment, which burrows into gravel, bearing rhizomous appendages and attaching to shell and gravel particles, or without rhizomes, and merely tightly adhered to dead coral or rock substrate. Stalk is variable in length (up to 12 cm long), free from surface conules and with woody texture. Basal stalk ranges from 8-24.5 mm (mean 13.4 mm) in diameter. Branches thinly or thickly cylindrical, bearing large conules. Average branch diameter ranges from 3.5-16 mm (mean 8.2 mm) excluding conules; 9.5-24 mm (mean 14.5 mm) including conules. Branching planar or multiplanar. Planar specimens from subtidal waters orientated with maximum surface area facing direction of currents; multiplanar subtidal specimens often found in crevices or in lee of coral heads. The orientation of deeper water specimens is unknown. Branching patterns variable, from dichotomously branched with repeated bifurcation, to simply digitate with few branches, or loosely reticulate with 1 or more anastomoses. Specimens range in size from 10-64 cm (mean 31.5 cm) high from basal attachment to apex of branches.

Texture: extremely tough, hard and woody texture at base, difficult to cut. Branches only slightly compressible, firm in texture. The ectosomal, pigmented layer more easily compressed than axis, which is more-or-less rigid.

Surface characteristics: optically smooth, microscopically hispid surface, with evenly distributed, prominent, tapering conules on all branches. Conules range from 2-4 mm (mean 2.6 mm) in diameter at their bases, and are 2-5 mm (mean 3.1 mm) high. Oscula minute and distributed evenly over surface. Pores visible in subtidal specimens *in situ* only by absence of silt immediately surrounding and radiating from them, due to water movement. Pores range from 0.2-1.0 mm in diameter in preserved specimens. Surface microscopically rugose, bearing a series of interconnected low-lying ridges, between which there are numerous pores.

Ectosome: dense, not translucent, and relatively easily detached. Ectosome contains heaviest concentrations of euasters, by comparison with subectosomal regions, and



Figs 13-16. Material from the British Museum (Natural History) (photos F. Wiedenmayer): 13, figured holotype of *Dictyocylindrus dentatus* Bowerbank (unregistered) (NMV 41/9 sponge archives: a junior synonym of *Axos cliftoni*); 14, *Axos elegans* label name — specimen BM(NH) 1886.8.25.557 (NMV 40/25 sponge archives) — close morphological resemblance to *A. cliftoni* s.s.; spiculation of *A. flabelliformis* s.s., of which it is a suggested synonym; 15, *Plunocolumella anchoratus* holotype BM(NH) 1871.5.12.1.342; (NMV 45/34 sponge archives); 16, *Axos flabelliformis* holotype BM(NH) 1883.1.25.8 (NMV 41/11 sponge archives).

pierced by extra-axial tracts of subectosomal styles, which radiate towards surface, and form a more-or-less continuous dermal palisade. Ectosomal spongin is heavily pigmented but mostly obscured by dense layer of euasters.

Choanosome: peripheral skeleton moderately dense, containing scattered euasters and extra-axial tracts of relatively thick styles, which radiate from dense axial core. Spongin abundant, heavily pigmented and granular. Subdermal cavities not common, not lined by fibre-spongin, although usually lined with euasters, and occur closer to axial core than periphery. Subectosomal spicule tracts 30-120 μm in diameter, cored by 4-10 rows of styles. Tracts do not appear to have fibre component associated with them. Tracts more or less at right angles to axial core and mostly plumose, diverging towards periphery. Spicule tracts rarely anastomosing. Thin flexuous raphidiform styles may be present, strewn between subectosomal

spicule tracts, but their presence/absence and abundance varies between specimens. Choanocyte chambers 18-35 μm in diameter, but they are difficult to discern due to high densities of euasters. Peripheral skeleton occupies nearly 50% of diameter of sponge in cross-section, near basal stalk. By comparison, axial component of branches diminishes towards apex of sponge. Central axis massive, irregular and stellate in cross-section, and irregularities of axis correspond with distribution of surface conules. Axis consists entirely of relatively thin styles. These megascleres core anastomosing fibres, which are only lightly invested with spongin. Styles mostly longitudinally orientated, running in the direction of branch growth, but closer to the periphery of the axial skeleton tracts of styles begin to diverge radially, giving rise to the extra-axial component of the skeleton. Styles forming axial skeleton appear to be shorter and thinner than those forming subectosomal tracts, but not distinctly so, and examples of each occur in both regions.

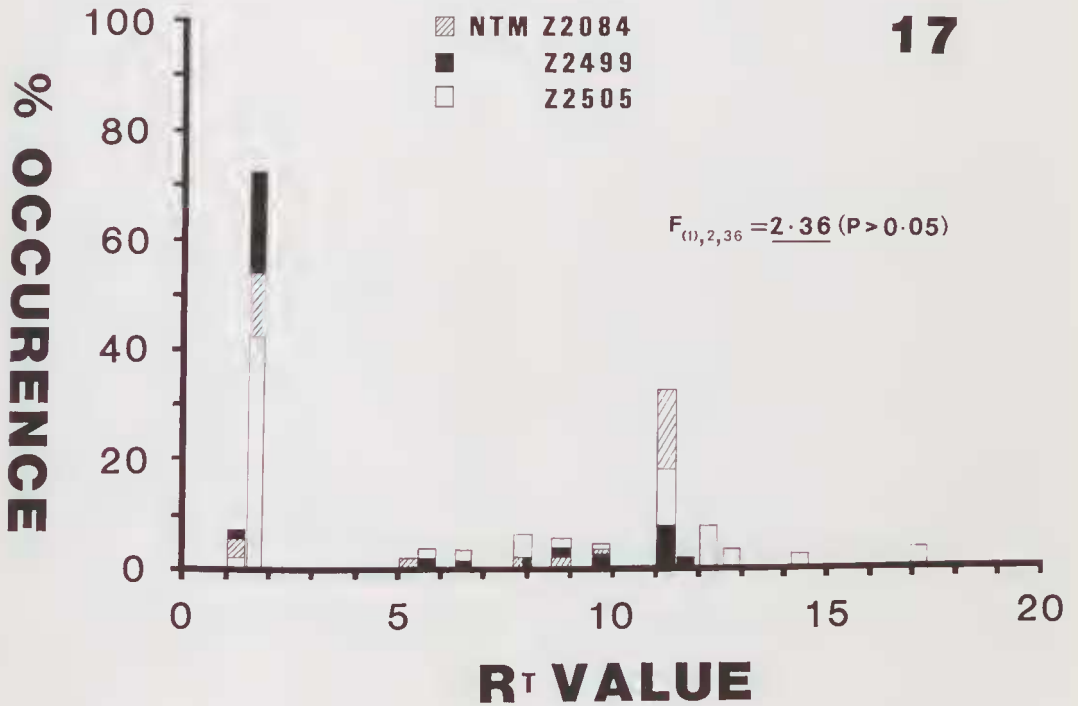


Fig. 17. Percentage occurrence of carotenoid pigments in 3 specimens of *Axos flabelliformis* (all bright orange, shallow-water morphs). Retention times (RT values) of major peaks were detected using normal phase High Pressure Liquid Chromatography and UV adsorption at 370 nm. Peak at RT 1.9 is probably authentic β -carotene (R. Capon, personal communication). Results of 2-way ANOV are given (Model II, without replication) showing level of significance.

Table 1. Summary of morphometric comparisons between *Axos cliftoni* and *A. flabelliformis*. Data show mean (± 1 standard error) and range of measurements. Results of statistical comparisons are given (R x 2 ANOV — Model II, and Student's t-test), showing levels of statistical significance.

CHARACTER	SPECIES	
	<i>A. cliftoni</i>	<i>A. flabelliformis</i>
STYLES		
Holotype		
Length:	517.68 μm (217-851 μm)	385.12 μm (193-691 μm)
Width:	9.08 μm (2-15 μm)	7.12 μm (2-12 μm)
Other		
Length:	474.59 μm (178-912 μm)	382.71 μm (118-795 μm)
		F=183.95 (P<0.0005)
Width:	11.07 μm (1.5-22 μm)	9.33 μm (0.8-28 μm)
		F=166.55 (P<0.0005)
EUASTERS		
Holotype		
Diameter:	23.36 μm (12-29 μm)	14.08 μm (9-21 μm)
Other		
Diameter:	24.27 μm (8-37 μm)	18.34 μm (4-29 μm)
		F=95.81 (P<0.0005)
GROWTH FORM		
Length:	630 \pm 15.3 mm (600-650 mm)	386.6 \pm 36.6 mm (120-640 mm)
		t(2), 16=2.89 (P<0.01)
Basal diameter:	18.3 \pm 3.85 mm (14-26 mm)	13.37 \pm 1.04 mm (8-24.5 mm)
		t(2), 16=1.77 (P>0.05)
Maximum branch diameter:	23.3 \pm 2.85 mm (15-35 mm)	14.5 \pm 0.52 mm (9.5-24 mm)
		t(2), 44=5.23 (P<0.001)
Mean branch diameter:	13.6 \pm 2.28 mm (7-22 mm)	8.21 \pm 0.42 mm (3.5-16 mm)
		t(2), 44=3.86 (P<0.001)

Megascleres: fusiform styles, straight or slightly curved near base, with sharply pointed or rounded apices, often with mucronate or stepped tips. Bases smooth, rounded, and without subtylote swellings or constrictions. (N=525) Length 382.71 μm (mean) (range 118-795 μm), width 9.33 μm (0.8-28 μm).

Microscleres: euasters, very variable in morphology, relatively small in size. Typically euasters hexaradiate, symmetrical, in 2 planes, with slightly swollen rays, bearing numerous minute microspines. (N=525) Maximum mean diameter 18.34 μm (range 4-29 μm).

Remarks. Burton (1934:549) placed *A. flabelliformis* into synonymy with *A. cliftoni*, without giving reasons. Burton may have been fully justified in his actions, on the basis of differences in characters between the two species known at that time. However, it has been shown above that *A. cliftoni s.s.* and *A.*

flabelliformis s.s. have marked differences in the morphology of euasters, and they are maintained here as distinct species for that reason alone (Figs 18-24). There is no correlation between habit and euaster morphology; indeed, no flabelliform examples of *A. flabelliformis*, apart from the holotype, are known. This separation is tenuous, and it is possible that euaster morphology is related to age of the sponge or conditions for growth. Other characters which do appear to be correlated with euaster morphology include branch diameter. *Axos cliftoni s.s.* has thickly cylindrical branches (mean diameter 13.6 mm), whereas *A. flabelliformis s.l.* is thinner and less rubbery in appearance (mean branch diameter 8.2 mm). This difference is significant at the 0.1% level (t_{(2), 44} = 5.23) (Table 1).

Biochemical evidence (carotenoid pigments and protein electrophoresis) is presently available for *A. flabelliformis* only

(Fig. 17 and unpublished data), but these data are merely descriptive without comparable results for *A. cliftoni*. The latter species is uncommon and known only from a relatively isolated locality in northwest Australia.

Other species associated with the genus

Three other species have been defined in *Axos*. Brief redescriptions and their affinities are as follows.

Latrunculia spinipoculum (Carter), comb. nov. (Figs 6-8)

Axos spinipoculum Carter, 1879: 286-291, Pl. 25, Figs 1-9.

Diacarnus spinipoculum — Burton 1934:549

Negombo spinipoculum — de Laubenfels 1936:132-3

Type material. HOLOTYPE - BMNH 1846.10.14.174 (wet: label "no 619, donated by J.B. Jukes Esq."; photograph NMV 34/1-2 sponge archives — F. Wiedenmayer).

Distribution. Type locality: Port Jackson, New South Wales (33°51'S 151°16'E) (Carter 1879).

Ecology. Growing "on hard objects" (Carter 1879). Depth unknown.

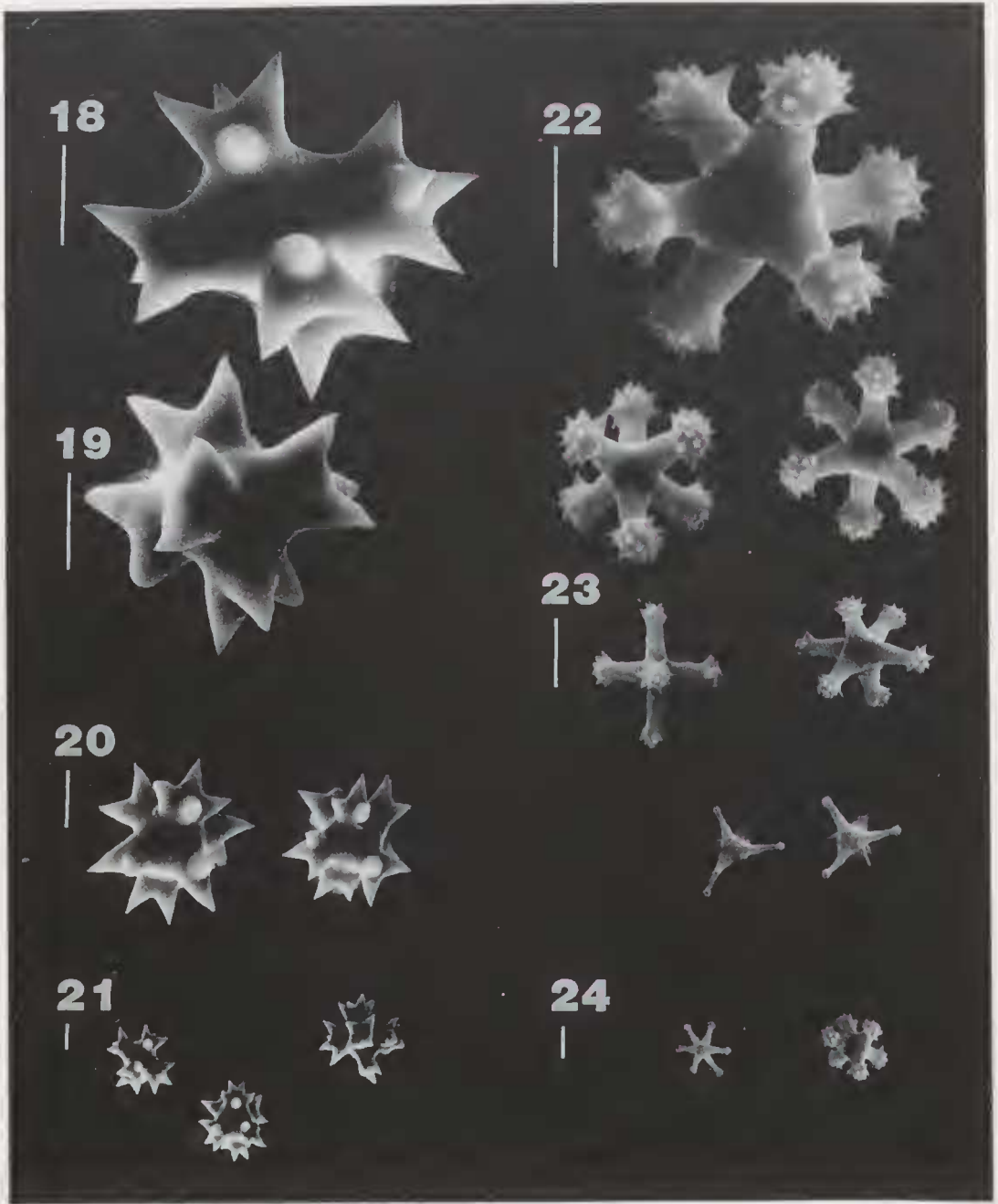
Description of holotype. Massive, elongate, subcylindrical, solid cup-shaped sponge, with an apical depression. Total length 14.5 cm from basal attachment to apex, 10.1 cm maximum diameter, 4.5 cm basal diameter. Basal end with holdfast adhering to gravel and shell fragments. No stalk. Surface highly ornamented with irregularly distributed ridges, depressions and conules, up to 15 mm high. Conules rounded, occasionally sharply pointed, up to 10 mm basal diameter. Surface optically smooth between ridges and conules, microscopically hispid. Minute pores scattered between surface projections. Oseula grouped together into sieve-plates, occurring on apical and exterior surfaces. Colour in preserved state is dark grey externally and beige internally. Texture tough and compressible. Ectosome spiculate, containing light paratangential brushes of choanosomal megascleres from ascending plumose tracts, which poke through surface. Ectosome and subectosomal regions are conspicuously more darkly pigmented than deeper regions. Few microscleres present in ectosomal or subec-

tosomal regions. Subectosome with distinct plumose, mostly non-anastomosing spicule tracts arising from choanosome and ascending to surface. Tracts diverge and form brushes, mainly in darkly pigmented peripheral region of sponge, which is up to 300 μm thick. Plumose tracts multispicular, heavily cored by megascleres (4-8 spicules per track). Subectosomal fibres well-developed and heavily invested with spongin (20-120 μm in diameter). Collagenous spongin filamentous, heavy and abundant throughout choanosomal region, resembling filamentous algal strands. Choanocyte chambers ovoid (25-50 μm diameter), but difficult to distinguish between collagenous filaments. Subdermal cavities abundant (65-190 μm diameter). Deeper regions of choanosome less well-organised, megascleres scattered between fibres. Fibres form tight meshes of irregular anastomoses. Microscleres scattered mainly throughout deeper regions of choanosome.

Megascleres: smooth, straight hastate styles, often with styloid and stepped tips. Basal ends rounded or slightly constricted. (N=25) Length 277.04 μm (mean) (range 232-305 μm), width 5.72 μm (4-7 μm).

Microscleres: verticillate sanidasters or discorhabd morphology, resembling a number of euasters fused onto a thin strongyle. Microsclere morphology and spination is relatively consistent, varying only in length and thickness. (N=25) Length 57.52 μm (40-65 μm), width 3.72 μm (2-6 μm).

Remarks. This species has been figured by Carter (1879), and his drawing is an accurate representation of the holotype. *Negombo* Dendy (type species *N. tenuistellata* Dendy, 1905: 127) is characterised in having peculiar "sanidaster" microscleres, consisting of a slender rod, terminating at each end with spines, and bearing slender spines along its length. Megascleres are smooth styles, and skeletal architecture consists of wispy plumose tracts throughout the choanosome, and a reticulation of styles on the surface. *Latrunculia* Bocage (type species *L. cratera* Bocage, 1869:161) is very similar (e.g. *L. conulosa* Hallmann, 1912:126), and I agree with de Laubenfels (1936) that the two genera are synonymous. *L. spinipoculum* has similar architecture to *N. tenuistellata*, but microscleres are much more regular than those of *Negombo* s.s..



Figs 18-24. Scanning electron micrographs comparing euasters of *Axos cliftoni* and *A. flabelliformis*: 18-21, *A. cliftoni* NTM 1274; 22-24, *A. flabelliformis*. NTM Z2499. All scale lines 10 μm .

In growth form and surface ornamentation, *L. spinipoculum* closely superficially resembles an *Ircinia* Nardo (order Dictyoceratida). By its spiculation, *L. spinipoculum* has affinities with *Sigmosceptrella* Dendy (type species *S. quadrilobata*

Dendy, 1922:137 from Mauritius), which has double asters or discorhabd microscleres and smooth styles as megascleres. *L. spinipoculum* is particularly close to *S. fibrosa* (Dendy, 1897:254; holotype NMV G2353), and it is possible, but not definite

that the two species are synonymous. Dendy's species has occasional, small sigmatose verticillate sanidasters, whereas those of *spinipoculum* are always straight. In any case, *S. fibrosa* should be transferred to *Latrunculia* also.

Unlike *N. tenuistellata*, *Sigmosceptrella* s.s. and *Latrunculia* s.s., the microscleres of *L. spinipoculum* and *L. fibrosa* do not form an ectosomal crust, but are more common in the deeper regions of the choanosome. However, this probably does not warrant the creation of a separate genus for the species (cf. *Diacarnus* Burton, 1934:549).

This species is certainly not closely related to *Axos* (cf. Carter 1879) or *Acarinus* (cf. Burton 1934) either by microsclere form or skeletal architecture. Nor are those microscleres typical of the discorhabds of *Latrunculia* s.s. or *Didiscus* Dendy, which have more pronounced discoid whorls, but rather they resemble several euasters fused onto smooth strongylote spicules. It is possible also that *Sigmosceptrella* is synonymous with *Latrunculia*, as suggested by Vosmaer (cited in Dendy 1922:137), and it is certainly probable that it should be placed with the Latrunculiidae Topsent, as suggested by Lévi (1973: 611).

The higher systematics of Latrunculiidae are uncertain. Dendy (1922), Bergquist (1978) and others place the family with the Hadromerids. Lévi (1973) includes it with the Pocillosclerids. Van Soest (1984: 146) follows Lévi, but defines the family as an *Ordo Incerta*. The skeletal architecture of *L. spinipoculum* described above is suggestive of the Pocillosclerida.

***Plumocolumella anchorata* (Carter)**

(Figs 9-10, 15)

Axos anchorata Carter, 1881: 382-383, Pl. 18, Fig. 3a-f.

Phorbos anchorata — Carter 1882: 288.

Plumocolumella anchorata — Burton 1934: 549-550.

Type material. HOLOTYPE - BMNH 1871.5.12.1.34a (slide; photograph NMV 45/35-36 sponge archives — F. Wicdenmayer).

Distribution. Type locality: Bass Strait, Victoria 39°S 145°E. Other: Turtle Island, Great Barrier Reef, Queensland, 22°21'S, 149°47'E (Burton 1934).

Ecology. Holotype found growing on a mussel shell. Queensland specimen recorded

from 16 m depth, in a mud and shell grit substrate.

Description of holotype. Thickly cylindrical, unbranched digit growing from an encrusting base. Basal stalk 4.1 mm in diameter, and maximum diameter of stalk 8.2 mm. Length of the whole specimen is unknown. Surface ornamented with small pointed conules and longitudinal ridges. Oscula scattered between conules. Colour alive is unknown, and brown in the dry state (NMV sponge archives 45/35-36, and Carter 1881). Texture is firm and compressible (Carter 1881:382). The choanosome is reticulate, formed of regularly anastomosing spongin fibres, without axial condensation or regional differentiation. Fibres cored by oxeas in multispicular tracts. Ectosome contains some megascleres at right angle to it, and piercing surface, particularly on conules. Microscleres scattered throughout mesohyal matrix.

Megascleres: oxeas, fusiform, mostly straight. (N=25) Length 265.34 μm (mean) (range 105-318 μm), width 8.44 μm (3-16 μm).

Microscleres: unguiferous anchorate isochelae. (N=25) Mean chord length 12.4 μm (9.5-21 μm).

Remarks. Regardless of their similarities in growth form (Fig. 15) (Carter 1881), *P. anchorata* bears little resemblance to *A. cliff-toni*. *Plumocolumella* Burton (type species *P. carnosa* (Carter, 1886)) is characterised by a choanosomal skeletal architecture consisting of plumose to plumo-reticulate fibres and tracts of oxeas, which terminate in brushes on the ectosome, and unguiferous anchorate

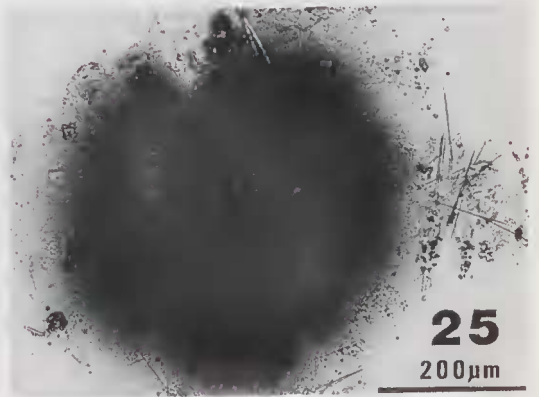


Fig. 25. Light micrograph of preserved larva of *Axos cliff-toni*, found in abundance on the external surface of the adult sponge, NTM Z1424.

isochelae and occasionally sigmas (Burton 1929:424). There is no evidence of distinct ectosomal brushes in the type specimen of *P. anchorata*, although single or few spicules pierce the ectosome in places, particularly at the apices of conules. Through its similarity with the type species, *P. anchorata* appears to be appropriately placed in that genus (cf. Burton 1934).

In possessing chelate microscleres and plumo-reticulate architecture, *Plumocolumella* is an obvious Poecilosclerid. Burton (1934) placed the genus in the Myxillidae Topsent, but more recently Van Soest (1984), following de Laubenfels (1936) and Lévi (1973) referred the genus to the family Desmacididae Schmidt (=Esperiopsidae Hentschel).

Gelliodes fibulatus (Carter)

(Figs 11-12, Pl. 1E)

Axos fibulata Carter, 1881: 383, Pl. 18, Fig. 4.

Phorbas fibulata — Carter 1882: 288.

Gelliodes fibulata — Ridley, 1884: 427, Pl. 39.

Fig. 1, Pl. 41, Fig. bb; Ridley and Dendy 1887: 47, Pl. 12, Fig. 2; Topsent 1897: 470, 1932: 114; Hentschel 1912: 393; Burton, 1934: 549; Lévi 1961: 141, Fig. 16; Wiedenmayer 1977a:95; Desqueyroux-Faundez 1981: 744, Figs 56, 117, 1984: 780-781, Figs 6, 51, 52, 58, 61.

Type material. HOLOTYPE - Lost from BMNH collection (Burton 1934: 549).

Additional material. NTM Z1000, East Point Fish Reserve, Darwin, NT, 12°24.5'S 130°48.0'E, 26 October 1982, 8-10 m depth, coll. J.N.A. Hooper, SCUBA; NTM Z1050, 9 November 1982, 13 m depth; NTM Z1445, Blue Hole, Gunn Point Reef, NT, 12°09.0'S 131°00'E, 19 August 1983, 25 m depth, coll. P.N. Alderslade, SCUBA; NTM Z980, NW Vernon I., Gunn Point, NT, 12°03.0'S 131°05.5'E, 27 September 1982, 15 m depth, coll. P.N. Alderslade, SCUBA; NTM Z48, Trepang Bay, Cobourg Peninsula Marine Park (CPMP), NT, 11°10'S 131°58'E, 16 October 1981, 1 m depth, coll. J.N.A. Hooper, by hand; NTM Z44, 11°07'S 131°58'E, 15 October 1981, 5 m depth, SCUBA; NTM Z357, Z349, Coral Bay, Port Essington, CPMP, NT, 11°11.2'S 132°03.6'E, 23 June 1981, 3-5 m depth, coll. J.N.A. Hooper, SCUBA; NTM Z53, 17 October 1981, 6 m depth; NTM Z79, 18 October 1981, 4 m depth; NTM Z1362, 1366,

1368, 1373, 16 May 1983, 0.5-5.5 m depth; NTM Z1392, 17 May 1983, 6 m depth; NTM Z105, Sandy I. No.2, CPMP, NT, 11°05.5'S 132°17'E, 20 October 1981, 7 m depth, coll. J.N.A. Hooper, SCUBA.

Distribution. Type locality: Bass Strait, Victoria, 39°S 145°E. Other: Torres Strait, North Queensland, 10°30'S 142°E; Northern Territory, 11-12°S 131-132°E; Ambon and Aru I., Indonesia, 4°30' - 6°S 128°05' - 134°20'E; Vietnam, 11°30'N 108°30'E; New Caledonia, 21°35'S 166°14'E.

Ecology. Bathymetric range 0.5-25 m depth. Commonly found growing on dead and live corals, and other sponges as an epizootic growth. Occasionally found on rock or sand substrates (present observations).

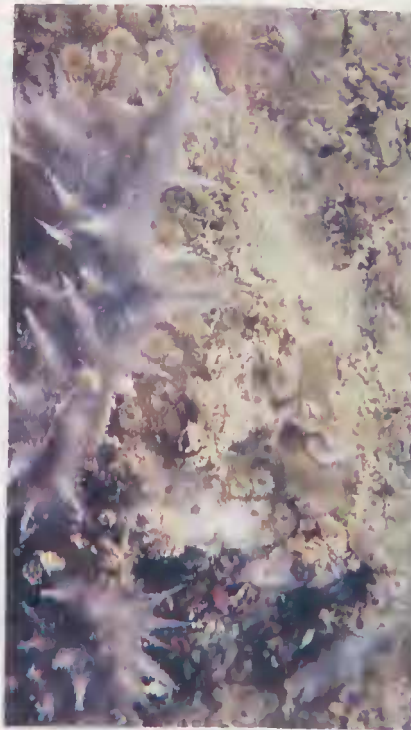
Description. Cylindrical digitate; anastomosing at multiple points of contact with substrate, and with meandering stoloniferous habit; variable in size. Colour in life grey to pale blue (Munsell 5G 8/2-2.5B 8/4) (Pl. 1E). Surface bears numerous, strong, slender, sharp spines, 4-13 mm long, upon which smaller secondary spines occur. Ectosomal region membranous, opaque, and contains an obvious, regular reticulation of multispicular tracts, through which protrude ascending primary and secondary choanosomal spicule tracts, forming spines. Choanosomal fibres heavily invested by spongin, and divided into ascending, relatively irregular primary lines, fully cored by multispicular tracts of megascleres (150-310 μm diameter), from which diverge multispicular secondary tracts (45-110 μm) at various angles, forming loose anastomoses and an open network (spaces up to 280-720 μm diameter). Non-fibre spongin relatively heavy in mesohyl matrix, with abundant, loosely strewn megascleres and microscleres. Choanocyte chambers oval, 80-150 μm in diameter.

Megascleres: very variable in thickness. Larger category smooth, hastate, mostly straight oxeads, with abruptly pointed apices, often with stepped tips. Smaller category fusiform, sharply pointed. (N=25) Length 264 μm (mean) (range 139-279 μm), width 11.8 μm (2-16 μm).

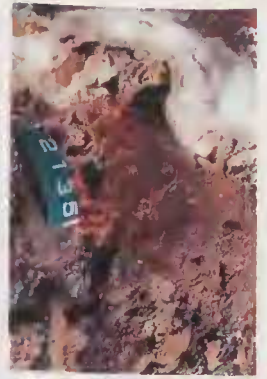
Microscleres: minute, thin smooth sigmas, invariably c-shaped, with slight (but not definite) tendency to be centrangulate. (N=25)



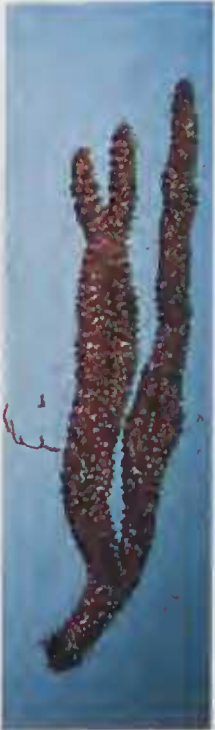
D



E



F



A



B



C

Plate 1. Marine Sponges: A, *Axos cliftoni*, NTM Z1821 "on deck", photo T. Ward; B, *Axos flabelliformis*, red colour morph, NTM Z1808, "on deck" photo T. Ward; C, *A. flabelliformis*, orange colour morph, NTM Z2688, *in situ*, photo J. Hooper; D, *A. flabelliformis*, beige colour morph, NTM Z1822, "on deck" photo T. Ward; E, *Gelliodes fibulatus*, NTM Z44, *in situ*, photo J. Hooper; F, *Timea lowchoyi* holotype, NTM Z2135, *in situ*, photo J. Hooper.

Mean chord length 13.6 μm (10-17 μm), maximum mean width 0.85 μm (0.5-1.2 μm).

Remarks. *G. fibulatus* is the type species of the genus (by monotypy; Ridley 1884). It is a well documented species, and from published accounts (Carter 1881; Ridley and Dendy 1887; Lévi 1961; Desqueyroux-Faundez 1981, 1984) and present observations, it is distinctive and easily recognizable (Pl. 1E), and easily differentiated from *Axos*. It is superficially characterised in having razor-sharp surface spines, which may vary considerably in length. The meandering, anastomosing stoloniferous habit, often with multiple points of attachment, appears to be usual for the species. Therefore, it is unlikely that *G. fibulatus* is synonymous with Lamarck's (1814-15) *Spongia rubispina* (as suggested by Ridley and Dendy 1887). The spiculation of Lamarck's species is unknown (the type specimen is missing; Topsent 1932: 114), but there is a significant variability in growth form between *G. fibulatus* and Lamarck's species (Desqueyroux-Faundez 1984).

For the Northern Territory specimens, *G. fibulatus* is often epizootic in habit. Its association with coelenterates and sponges appears to be deleterious to the host/substrate, usually causing etching of live coral or necrotic spots on sponges. However, damage is minimal and localized to the points of contact only. This association is comparable to that of *Sigmatocia symbiotica* Bergquist and Tizard (= *Gellius cyniformis* (Esper)) (see *a.o. Vacelet*, 1981)) (Haliclonidae, Haplosclerida) from Northern Australia, which has been observed to kill square metres of live coral (personal observation).

In the most recent revision of the Haplosclerida (Van Soest 1980; Desqueyroux-Faundez 1984), *Gelliodes* is placed with the Niphathidae Van Soest. By comparison, Lévi (1973) and Wiedenmayer (1977a) include it with the Haliclonidae de Laubenfels.

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